Journal of Herpetology, Vol. 33, No. 2, pp. 281–291, 1999

Nightly and Seasonal Movements of *Boiga irregularis* on Guam

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ABSTRACT.—**Brown tree snakes (*Boiga irregularis,* BTS), inadvertently introduced to the island of Guam shortly after World War II, have had catastrophic effects on the native fauna of this U.S. territory. We used radio-telemetry to monitor daytime refugia and nightly movements of 60 BTS (30 during each of two seasonal periods) to determine the extent of nightly, weekly, and monthly movements. Eighty-three percent of subadult daytime sightings were in trees, compared to only 49% of adult daytime sightings. Most measures of movement did not vary with seasonal period, sex, or age class. BTS moved an average of 64 m (Range: 9–259 m) between successive daily refugia. Mean total cumulative distance traveled between successive locations from one afternoon to the next was 238 m during January–March and 182 m during May–July. However, over the course of each seasonal period (60–70 d), most snakes concentrated their activity within core areas. During each of the two seasonal periods, snakes were located a mean distance of only 78 m and 93 m, respectively, from their original release points 30–50 d after release. Sixty to 70 d after release, snakes were a mean distance of 92 m and 68 m, respectively, from their original release points. Snakes frequently crossed dirt roads that separated forested areas at the study site. They also utilized grassy and brushy clearings, but less than would be predicted by the occurrence of such clearings in the study area. These results suggest that under the conditions of this study, BTS would be slow to reinvade areas where snakes have been removed by trapping or other means.**

Brown tree snakes (*Boiga irregularis,* BTS) are native to eastern Indonesia, New Guinea, the Solomon Islands, and parts of Australia, but were inadvertently introduced to Guam shortly after World War II (Rodda et al., 1992). The subsequent irruption of this species on Guam has had an impact both on the economy and on the native fauna of the island. BTS climb electric power lines, causing power outages (Fritts et al., 1987), have been a major catalyst in the demise of Guam's native fauna (Savidge, 1984, 1987; Conry, 1988; Engbring and Fritts, 1988; Rodda and Fritts, 1992), and attack pets, poultry, and people (Fritts et al., 1990, 1994; Fritts and McCoid, 1991).

There is an appreciable threat that BTS will spread from Guam and threaten the faunas of other Pacific islands (Fritts, 1987; Rodda et al., 1997). This nocturnal reptile often seeks cover during the day in dark, inconspicuous refugia such as cargo containers, washing machines, automobiles, and even the wheel wells of aircraft. This propensity increases the probability that BTS will become passive stowaways aboard the abundant air and maritime traffic that originates or passes through Guam. Transplanted BTS have been discovered on Saipan, Okinawa, Kwajalein, Diego Garcia, Oahu, and Texas (McCoid et al., 1994; Fritts, 1988).

Federal, state (Hawaii), and territorial governments (Guam and the Commonwealth of the Northern Mariana Islands) have expended much money and effort to reduce BTS populations around ports of entry and exit, endangered species breeding sites, and other critical areas (U.S. Department of Agriculture, 1996). Capturing BTS with funnel traps and removing them from fences where they congregate at night are the most commonly used methods of reducing BTS populations on Guam. U.S. Department of Agriculture/Wildlife Services (USDA/WS) personnel also use dogs to detect snakes in outgoing cargo (Engeman et al., 1998b). However, there is a growing consensus that additional and improved methods are needed to meet the challenge posed by BTS (Brown Tree Snake Control Committee, 1996).

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The U.S. Geological Survey, Biological Resource Division and Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center currently are conducting research to develop exclusionary fences, toxicants and delivery systems (Brooks et al., *in press*; Savarie et al., *in press*), and improved trapping techniques (Engeman et al., 1998a; Linnell et al., 1998).

A better understanding of BTS activity and movements would facilitate more effective use of control materials, particularly traps or toxicants. Knowledge of BTS movements in a typical night, week, or month and whether snakes utilize restricted areas (vs. random movement) would help determine the optimum density and placement of traps or baits. Knowing whether BTS cross roads or utilize cleared, grassy areas might indicate the optimal placement of control materials around ports, airfields, or other high priority areas. Likewise, determination of seasonal variation in movement would provide information on the most effective density and placement of baits during different seasons.

Little is known about the movements of BTS. Analyses of electrical outages caused by BTS and of snake-bite data indicate that these snakes are most active at night and during the rainy season from May through August (Fritts et al., 1987, 1994). Radio-telemetry studies (Wiles 1986, 1987; Santana-Bendix et al., unpubl. data) have shed some light on nightly snake movements. These studies did not investigate seasonal variation and were based on only a few adult snakes. Recent technological advances have allowed reductions in the size of radio transmitters, thus allowing the study of smaller snakes more typical of wild populations on Guam (Savidge, 1991). Therefore, during each of two periods that are normally representative of the wet and dry seasons on Guam, we monitored the movements of a larger sample of BTS constituting a broader size range than in previous studies. Our objectives were (1) to determine the extent of nightly, weekly, and seasonal movements during the two seasonal periods, (2) to determine whether BTS utilize circumscribed areas, and (3) to detect changes in movement patterns in ecotones of forests and adjacent open areas or clearings.

Materials and Methods

Study Area.—We conducted the study in the Munitions Storage Area, southeast of an area called "Northwest Field", on Andersen Air Force Base (AAFB), near the northernmost tip of Guam. The Munitions Storage Area comprised 525 ha of secondary growth forest on limestone-derived soils that had a scattered, discontinuous canopy and dense subcanopy and understory vegetation. A grid of compacted limestone roads divided the area into rectangular sections that were about 800 m long and 100 m wide. Six to seven square cleared areas approximately 0.25 ha each and consisting of grasses and shrubs <1 m tall extended about 50 m into the east side of each section. Common overstory plants included *Vitex parviflora, Cycas circinalis, Pandanus* spp., and *Neisosperma oppositifolia. Guamia mariannae, Hibiscus tiliaceus,* and *Triphasia trifolia* permeated the subcanopy layer. Understory ground vegetation grew on shallow, well-drained cobbly clay loam over porous limestone rocks and included ferns (*Asplenium* spp., *Polypodium* spp., *Pteris* spp.), vines, and small herbs (*Peperomia* spp., *Pilea* spp.). Skinks (*Carlia fusca, Emoia* spp.) and geckos (*Lepidodactylus lugubris, Hemidactylus frenatus*) were common throughout Guam (Rodda and Fritts, 1992; Campbell, 1996). Rats (*Rattus* spp.), sambar deer (*Cervus unicolor*), and feral pigs (*Sus scrofa*) were common throughout the study area. We captured, released, and observed BTS in four adjacent sections comprising 65 ha in the interior of the Munitions Storage Area.

Capture of Snakes.—BTS were captured with cylindrical, wire-mesh traps that had an inward pointing funnel and a one-way flap door at each end (Fritts, 1988; Linnell et al., 1998). Each trap was baited with a live mouse (*Mus musculus*) that was provided with rodent chow and fresh potatoes and protected within a wire-mesh compartment in the center of the trap. A piece of plastic or waxed paper covered the compartment and protected the mouse from direct exposure to rain and direct sunlight. Traps were set 0.5–2 m above the ground in the crotches of trees within 10 m of a road or grassy, cleared area. We checked traps daily before 1000 h.

Implantation of Radio Transmitters.—We transported traps with snakes about 3 km from the Munitions Storage Area to the USDA/WS kennel facility on AAFB for implantation of radio transmitters. We anesthetized snakes with halothane (Fowler, 1995), measured the length from snout to vent (SVL), and probed for hemipenes to determine sex (Jordan and Rodda, 1994). We then followed the methods of Reinert and Cundall (1982) for implanting miniature radio transmitters. We inserted the antenna subcutaneously and used Duro Super Glue® (Loctite Corp., Newington, CT) to close the incision. We used a chromic gut suture to anchor the transmitter to the peritoneal wall. After implantation of transmitters, snakes were placed in opaque plastic containers and held until sunset (4–5 h after surgery), when they were released at their original capture sites.

Each radio transmitter (Holohil Systems, Ontario, Canada) weighed 1.4 g, was 7.0 mm × 5.0

mm × 17.0 mm, had an 18-cm wire whip antenna and a battery life of 40–50-d, and transmitted 50–70 pulsed signals per minute in the 164–167 MHZ range.

We monitored two groups of snakes, one between 19 January and 27 March 1996, which normally is considered the dry season on Guam, and one between 29 May and 9 August 1996, which usually coincides with the transition from the dry to the rainy season. However, 1996 was unusual in that the rainy season did not commence until mid-July. We began monitoring the locations of snakes two weeks after release during January-March and one week after release during May–August. Transmitter failure (indicated by the loss of one signal) or mortality (indicated by a continuous stationary signal from under a log) resulted in the loss from the study within a week of release of two BTS during January–March.

Daytime Refugia.—We visually located the daytime refugium of each BTS twice during the study by using a hand-held 3-element, collapsible Yagi antenna (Wildlife Materials®, Carbondale, IL) and a portable radio receiver (CE-12 Custom Electronics®, Urbana, IL) to follow the snake's directional radio signal to its source. We attempted to confirm the presence of each snake visually, although frequently snakes were high in the canopy, ensconced inside hollow limbs, or otherwise hidden from sight. Geographic locations of refugia were determined by use of a Global Positioning System (GPS) receiver (GeoExplorer, Trimble Navigation®, Sunnyvale, CA) mounted on a 6-m telescoping fiberglass pole extended above the forest canopy. For each refugium, we recorded substrate (e.g., species of vegetation, dead log, surface of ground) and height of refugium above ground.

Vegetation Sampling.—To estimate the density and frequency of plant species in the study area, we sampled vegetation at five points along each of two transects in each of the four sections in the study area, for a total of 40 sampling plots. Transects extended perpendicularly between the roads that bordered the longer sides of the sections. We randomly determined the starting location of each transect along the road, divided the transect into five equal segments, and randomly determined the location of the first sampling point within the first segment. The distance between subsequent samples along the transect was equal to $\frac{1}{5}$ of the length of the transect.

We used the point-centered quarter method (Mueller-Dombois and Ellenberg, 1974) to sample vegetation in each of four 90-degree quadrants emanating out from each sampling point. The boundaries of the quadrants were determined by spinning a cross constructed of two intersecting, perpendicular sticks. In each quadrant, we measured the distance from the sample point to the nearest plant that was ≥2 m tall and had a basal diameter ≥2 cm. We recorded the species of vegetation and used a cloth tape to measure the basal height (circumference 1.5 m above the ground). Where trunks forked below 1.5-m, we measured the diameter of the fork nearest to the sampling point.

Nightly Movements.—Repeatedly trampling through thick vegetation with a machete would modify the habitat (Nickerson et al., 1978) and potentially modify snake behavior. Thus, we monitored nocturnal locations of snakes by triangulation. During each seasonal period, we recorded the locations of each telemetered snake during five 24-h tracking sessions that each extended from the afternoon of one day through the afternoon of the following day. We divided the snakes into two groups of 15 each and monitored only one group during any given tracking session. We alternated between groups during the 10 tracking sessions.

We determined the location of each snake five times during a tracking session: once between 1200 h and 1500 h, three times between sunset and sunrise (usually once each between 2001 and 2200 h, 2300 and 0100 h, and 0201 and 0400 h), and once between 1200 h and 1500 h the following day. We assumed that the afternoon readings indicated the refugia used by snakes before and after their nightly activity period (Santana-Bendix et al., unpubl. data).

For each BTS location, we attempted to determine triangulation bearings from ≥4 pre-established permanent locations along the roads of the study area. Two people in separate pickup trucks used two-way VHF FM hand-held transceivers (Bendix-King, Lawrence, KS) to coordinate readings and to determine optimal points for obtaining triangulation fixes. All fixes for each estimated location were taken within one hour of each other.

We used hand-held GPS receivers and related software to determine the geographic positions of the pre-established reference locations from which we took bearings. We differentially corrected the locations with data from a known reference station 5 km away (Rempel and Rodgers, 1997). Our estimate was <2 m from true.

The accuracy of our triangulation fixes was determined by the location error method of Zimmerman and Powell (1995). At various times throughout the study, we used a single blind placement whereby a person who was not tracking the snakes placed transmitters similar to those implanted in the BTS at locations distributed throughout the study area. The transmitters were placed in exposed locations on tree branches or on the ground; in hollow logs; on the ground under leaves, logs, or rocks; and in other concealed locations. We took fixes on the human-placed transmitters during the same tracking sessions in which we triangulated on the locations of snakes. After each tracking session, we subsequently followed the directional signals of the human-placed transmitters to their sources and used a 6-m telescoping fiberglass pole to elevate a GPS receiver above the canopy and determine true geographic locations.

Data Analyses.—LOCATE II radio-telemetry triangulation and plotting software (Pacer Computer, Truro, Nova Scotia) was used to plot bearings and estimate snake locations. We estimated each fix by using the combination of bearings that resulted in the smallest 95% ellipse home range. We estimated nightly movements for each snake as the total cumulative distance between successive locations from one afternoon to the next (i.e., original refugium to first night location to second night location to third night location to subsequent next-day refugium). We estimated movements during different periods of night and day as the distance between consecutive locations divided by the time elapsed between when those locations were recorded. We estimated movements over longer periods by calculating the shortest distance from where each BTS was released to its location 30–50 d and 60–70 d later. We estimated the extent of each snake's movements during each seasonal period by calculating the median distance of its observed locations from its calculated central point (mean x and y coordinates, MDIS) (White and Garrott, 1990, pp. 134). SAS statistical software (SAS Institute Inc., 1989a, b) was used to perform all analyses. We used PROC ANOVA to detect differences in the distance between triangulated and GPS-determined locations of transmitters placed by humans in various locations. We performed separate PROC GLM analyses to detect differences between seasonal periods, sexes, and age classes with regard to (1) distance between refugia used on successive days, (2) total cumulative distance between successive locations from one afternoon to the next, (3) MDIS, (4) distance of snakes from their release points 30–50 d and 60–70 d after release, (5) percentage of consecutive observations that were on opposite sides of a road, and (6) percentage of sightings that were in clearings. To compare seasonal periods, we evaluated MDIS only for 15–21 d and 22–30 d after release. We used PROC MIXED with repeated measures on individual snakes to detect differences between sexes, seasonal periods, and times of night (early vs. late) with regard to mean distance between consecutive locations (adjusted for time elapsed between observations). Duncan's multiple range test with an experiment-wise error rate of 0.05 was used to separate means (Saville, 1990). We used a multiresponse permutation procedure (MRPP; Mielke et al., 1981) and BLOSSOM statistical software (Slauson et al., 1991) to detect spatial shifts in areas of utilization over the course of each seasonal period; the procedure tested whether locations from three time intervals during each seasonal period came from a common density distribution.

We performed chi-square goodness of fit analyses to compare the number of diurnal observations associated with each species of plant during each seasonal period to the relative frequency of that species in the study area. Because of small sample sizes for some species of plants, we pooled data for all snakes during each season, without regard to potential individual snake preferences. We evaluated movements at ecotones by (1) calculating the percentage of BTS that crossed roads after being released along roads at the edge of forests, and (2) comparing the percentage of BTS locations that were within cleared, grassy areas to the overall percentage of area encompassed by open clearings. We examined the effects of precipitation on snake movements by Pearson's product-moment correlation coefficient (SAS Institute Inc., 1989b) to detect any relationships between total cumulative distance moved from one afternoon to the next and total cumulative rainfall during the previous 24, 48, 72, and 96 h.

Results

We captured 11 juvenile (SVL $\leq$ 980 mm; Rodda et al., 1998) and three adult (SVL $>$ 980 mm) male BTS and 14 juvenile and four adult female BTS during January-March, and six juvenile and five adult male BTS and eight juvenile and 11 adult female BTS during May–August. Mean snout-vent length of snakes was 894.3 mm (range: 725.0–1089.0) during the former period and 951.3 mm (range: 628.0–1100.0) during the latter (ANOVA $F = 3.69$, df = 1,58, $P = 0.06$). Mean SVL was 923.0 mm for males and 921.1 mm for females (ANOVA $F = 0.04$, df = 1,58, $P = 0.84$).

Triangulation Accuracy.—We were able to estimate locations for 12 of 16 test transmitters that were placed on branches in trees, two of five transmitters that were left exposed on the ground, four of five transmitters that were placed under logs, rocks, or other debris on the ground, seven of nine transmitters that were placed in hollow logs, and one of two transmitters that were concealed in metal munitions pallets stored on the ground in the cleared areas. Excluding the unreplicated pallet location, accuracy of triangulation varied with placement

TABLE 1. Daytime (1200 h–1500 h) locations of brown tree snakes monitored by radio telemetry in a secondary growth forest on Andersen Air Force Base, Guam, 1996.

Seasonal period	Location	Subadults N	Subadults % of sightings	Adults N	Adults % of sightings
January–March	tree	24	83.0	6	30.6
	ground		2.1		61.1
	dead log		12.8		8.3
	ammo pallet		2.1		0
May–August	tree	14	92.8	16	67.7
	ground		3.6		17.7
	dead log		3.6		14.6

(ANOVA F = 4.71, df = 3,26, P = 0.009). The discrepancy in mean distance between triangulated and GPS determined locations was greater (DUNCAN $P < 0.05$) for transmitters covered or buried under debris on the ground (47.6 m, SE = 8.5, N = 4) than for transmitters placed in trees (24.3 m, SE = 3.4, N = 13) or exposed on the ground (26.1 m, SE = 6.1, N = 5). The mean distance between triangulation and GPS locations did not differ (DUNCAN $P > 0.05$) between transmitters placed in hollow logs (40.7 m, SE = 4.7, N = 8) and those buried on the ground.

Daytime Refugia.—We visually identified an average of two daytime refugia per BTS. Juveniles utilized arboreal refugia 83% and 93% of the time during the two seasonal periods, compared to only 31% and 68%, respectively, for adults (Table 1). Several species of trees and shrubs were used as arboreal refugia (Table 2). BTS usage of the different species occurred in proportion to their relative frequency in the study area during January–March (χ^2 = 3.82, df = 5, P = 0.26) but not during May-August (χ^2 = 16.89, df = 5, P = 0.005). During the latter period BTS utilized *Pandanus* more often than the relative frequency of this plant in the study area would suggest if plant species were used at random (χ^2 = 10.51, df = 1, P = 0.001; Table 2).

Refugia used by the same BTS on consecutive days were spaced at distances averaging 64.4 m (SE = 4.7, N = 60). This distance did not vary between seasonal periods (ANOVA F = 0.58, df = 1,52, P = 0.45), sexes (ANOVA, F = 1.27, df = 1,52, P = 0.27), or adults and juveniles (ANOVA, F = 0.03, df = 1,52, P = 0.86). Based on x and y coordinates calculated by triangulation, we observed no instances in which the same BTS used the same refugium on consecutive days. However, 22% of successive estimated locations of refugia were within the approximate error distance of triangulation estimates for test transmitters exposed on branches or on the ground (25 m), and 50% of successive estimated refugia were within the approximate error for test transmitters placed in hollow logs or covered on the ground (50 m).

Movements.—Nightly snake movements as measured by total cumulative distance between successive locations from one afternoon to the next (i.e., original daytime refugium to first night location to second night location to third night location to subsequent next-day refugium) were marginally greater during January–March (238.1 m) than during May–August (182.2 m) (ANOVA, F = 3.27, df = 1,49, P = 0.08). Nightly movements did not vary between sexes (ANOVA, F = 0.08, df = 1,49, P = 0.78) or between adults and subadults (ANOVA, F = 0.20, df = 1,49, P = 0.66).

Mean distance per hour between consecutive locations (i.e. distance adjusted for time elapsed between observations) was similar for males

TABLE 2. Relative frequency of plants in study area,[a] mean percent of arboreal observations in each species of plant, and mean height of 30 brown tree snakes above ground in a secondary growth forest on Andersen Air Force Base, Guam, 1996. [a] Relative frequency = ([no. points with species/total no. points]/Σ[relative frequency of all species]).

Species	Relative frequency	January–March % of arboreal observations	January–March Height of snake Mean (m)	January–March Height of snake SE	May–August % of arboreal observations	May–August Height of snake Mean (m)	May–August Height of snake SE
Guamia mariannae	26.4	38	3.6	0.19	29	2.9	0.21
Pandanas spp.	7.5	8	4.8	0.83	18	2.7	0.57
Triphasia trifolia	9.4	8	2.6	0.30	16	2.2	0.28
Vitex parviflora	17.9	20	4.5	0.37	13	3.4	0.27
Cycas circinalis	11.3	8	2.3	0.33	3	2.0	—
Other	27.5	18	3.3	0.51	21	2.0	0.30
TOTAL	100.0	100	3.6	0.19	100	2.6	0.14

TABLE 3. Mean distance per hour between consecutive locations of brown tree snakes located by radio telemetry five times between two consecutive afternoons in a secondary growth forest on Andersen Air Force Base, Guam, 1996.

Time of readings (h)		January–March			May–August		
First	Second	N	Mean distance (m) per hour	SE	N	Mean distance (m) per hour	SE
1201–1500	2001–2200	30	8.4	0.7	29	6.6	0.6
2001–2200	2301–0100	29	15.2	1.7	29	15.9	1.4
2301–0100	0201–0400	28	16.9	1.8	29	12.8	1.3
0201–0400	1201–1500	28	6.9	0.6	29	4.9	0.4

and females (ANOVA, F = 0.04, df = 1,55, P = 0.84), was slightly greater during January-March than during May-August (ANOVA, F = 3.15, df = 1,55, P = 0.08), and varied among times of day (ANOVA, F = 39.12, df = 3,161, P = 0.0001). Distances were similar (DUNCAN $P >$ 0.05) between consecutive locations recorded between 2001–2200 h, 2301–0100 h, and 0201–0400 h, and were greater (DUNCAN $P < 0.05$) during these times than for consecutive readings taken between 0201–0400 h, 1201–1500 h, and 2001–2200 h (Table 3). Distances did not differ (DUNCAN $P > 0.05$) for consecutive locations taken during the latter three periods.

Distance of snakes from their release points 30–50 days and 60–70 d after release did not vary between seasonal periods (ANOVA, F = 0.08, df = 1,50, P = 0.78) or time elapsed after release (ANOVA, F = 0.44, df = 1,25, P = 0.51). During the January–March tracking session, BTS were a mean distance of 77.8 m (SE = 13.5, range: 12.1–378.8, N = 30) from their original release points 30–50 d after we released them and 92.1 m (SE = 16.7, range: 23.2 to 389.7, N = 22) from their release points 60–70 d after release. During the May–August tracking session, BTS were located a mean distance of 93.0 m (SE = 21.1, range: 19.0 to 438.2, N = 22) and 68.2 m (SE = 29.9, range: 1.2–175.0, N = 5), respectively, from their original release points 30–50 and 60–70 d after release.

TABLE 4. Average median distance (m) of observed locations for individual brown tree snakes from that snake's calculated central point in a secondary growth forest on Andersen Air Force Base, Guam, 1996.

Days after release	January–March		May–August	
	N	Median distance (m)	N	Median distance (m)
6–14	—	—	30	50.4
15–21	30	37.8	30	35.8
22–30	30	49.9	28	38.5
31–40	28	46.1	—	—

Movements as measured by MDIS were similar between sexes (males: 57.1 m, females: 54.0 m) (ANOVA, F = 0.25, df = 1,52, P = 0.62) and age categories (adults: 55.7 m, subadults: 54.9 m) (ANOVA, F = 0.28, df = 1,52, P = 0.60) but were greater during January–March (55.2 m) than during May–August (42.1 m) (ANOVA, F = 5.42, df = 1,52, P = 0.02). For the latter comparison, we considered only the time intervals that were common to the two seasonal periods (i.e., days 15–21 and 22–30 after release). Within each seasonal period, MDIS varied over the course of the May–August session (ANOVA, F = 3.66, df = 2,85, P = 0.03) but not the January–March session (ANOVA, F = 2.18, df = 2,85, P = 0.12) (Table 4). During the former period, MDIS was significantly greater (DUNCAN $P <$ 0.05) during the interval 6–14 d after release than during the intervals 15–21 or 22–30 d after release (Table 4).

We saw no evidence that BTS shifted their weekly areas of utilization during the 40 d in January–March (MRPP P = 0.98) or 30 d in May–August (MRPP P = 1.00) that we intensively monitored their movements.

Forty-six of 60 BTS were known to have crossed a road at least once. The percentage of consecutive observations that were on the opposite sides of a road varied considerably among snakes, from 0 to 37%. Overall, the mean percentage of consecutive locations that were on opposite sides of a road was 14.5% during January–March and 10.2% during May–August (ANOVA, F = 5.29, df = 1,52, P = 0.02). Frequency of road crossings did not vary by sex (ANOVA, F = 1.76, df = 1,52, P = 0.19) or size class (ANOVA, F = 0.07, df = 1,52, P = 0.79).

We located 44 of the 60 snakes in grassy clearings at least once during the study. A mean of 7.7% and 8.8% of all observations for individual snakes were in grassy clearings during January–March and May–August, respectively. Fewer observations were located in clearings during the two seasons than would be predicted based on the 25% of the study area that encompassed such areas ($\chi^2 = 22.47$, df = 1, $P < 0.005$). The percentage of sightings in clearings did not vary by seasonal period (ANOVA, F = 0.19, df = 1,52, $P = 0.66$), sex (ANOVA, F = 0.07, df = 1,52, $P = 0.79$), or size class (ANOVA, F = 0.75, df = 1,52, $P = 0.39$).

Forty-nine centimeters of rain fell during January, February, and March; and 63 cm fell during May, June, and July. We detected no relationship between nightly movements and cumulative precipitation during the previous 24, 48, 72, or 96 h ($r^2 < 0.01$, $P > 0.11$).

DISCUSSION

Daytime Locations.—During daylight hours, we most often found BTS 2.0–5.0 m above the ground in *Guamia*, *Pandanus*, or other plants common in the study area. Santana-Bendix et al. (unpubl. data) followed the movements of 11 BTS near our study area and also found that they commonly took refuge >2.5 m above the ground, most frequently in *Pandanus* trees. Wiles (1986) tracked a female BTS on Guam for 22 d and reported that 82% of day sightings were in the upper canopy. Arboreal refugia may provide a favorable microclimate for foraging (Lillywhite and Henderson, 1993), thermoregulation (Peterson et al., 1993), water retention (Lillywhite and Henderson, 1993), and/or protection from predation (Shine and Lambeck, 1985; Shine and Fitzgerald, 1996).

Adults in our study frequently took refuge on the ground during the day. Wiles (1987) monitored the movements of two BTS that rested exclusively on or under the ground during the day, and attributed this behavior in part to a lack of suitable arboreal hiding places. As many as half of the adult daytime sightings in our study were on the ground in spite of an abundance of apparently suitable arboreal hiding places. Selection of refugia undoubtedly depends on more than the availability of suitable vegetation.

Brown tree snakes are opportunistic predators that are not limited to foraging in specific habitats or forest strata (Rodda et al., 1997). Their behavior depends in part on the relative abundance of arboreal and terrestrial prey. We do not know to what extent daytime refugia reflect foraging habits because we could not identify substrates or heights of nighttime locations, which were determined by triangulation from the roads. However, several other investigators have reported ground foraging by BTS. Rodda (1992), using a night vision device, encountered foraging BTS at heights 2–5 m above the ground less often than would be expected based on search effort, and reported a modal foraging height of less than 0.5 m. Rodda et al. (1998) related ground-foraging by BTS to the abundance of skinks and speculated that the diet of BTS on Guam has changed in recent years in response to the disappearance of endothermic prey. Campbell (1996) also reported a high incidence of BTS predation on terrestrial skinks.

The propensity of juvenile BTS to use arboreal refugia during the day, while adults often rested on the ground, might reflect different foraging strategies employed by these two age classes. Ontogenetic dietary shifts have been documented in a variety of snakes in the genus *Boiga* (Greene, 1989), including BTS. Savidge (1988) found that small- to medium-sized BTS consumed mostly small lizards, and larger BTS foraged on birds and mammals.

The support offered by foliage also determines spatial and ontogenetic foraging patterns of arboreal snakes (Lillywhite and Henderson, 1993). Many species of arboreal snakes, in the course of their development, must make allowances for increases in body mass and a declining ability to forage on unstable substrates. Henderson (1993) reported that smaller *Corallus enydris* in the West Indies subsisted primarily on *Anolis* lizards, which sleep on exposed vegetation, while adult *Corallus enydris* fed exclusively on endothermic prey. Henderson and Horn (1983) observed that in Haiti terrestrial prey made up a relatively greater proportion of the stomach contents of *Uromacer frenatus* that were ≥70 cm SVL compared to smaller snakes, and suggested that large snakes concentrate on large ground-dwelling lizards because they cannot stalk small- to medium-size climbing lizards on slender branches.

Our estimated mean distances between successive refugia are similar to those reported for BTS in other studies. This distance is a conservative estimate of how far snakes moved because some animals travel extensively during the night but return to the vicinity of the refugia they used the previous day (Laundré et al., 1987). Snakes in our study moved an average of almost 65 m between successive daytime refugia. Santana-Bendix et al. (unpubl. data), using larger BTS, recorded a mean distance of 55 m but noted that snakes frequently were inactive for several days. Wiles (1986, 1987) recorded average movements of <60 m between successive daytime refugia. During one year, Wiles (1987) monitored the movements of two BTS, one that changed daytime refugia during 8 of 10 d and another that utilized two underground refugia exclusively for 25 d. Our estimates of distances between successive refugia varied from 9 to 259 m. Because of the error associated with our triangulation estimates, some refugia that were identified as different locations actually may have been the same. Half of our estimated locations for successive daytime refugia were within 50 m (the approximate error associated with hidden test transmitters) of each other, and 22% were within 22 m (the error associated with exposed test transmitters).

Movements.—Capturing and handling the snakes, the surgical procedures, and the implanted transmitters themselves may have influenced the movements of the snakes. Worm snakes (*Carphophis vermis*) introduced into new sites in Kansas often moved long distances after release (Clark, 1970). Movements of timber rattlesnakes (*Crotalus horridus*) with implanted radio-transmitters also were greatest immediately following release, and declined to a steady level 20–25 d later (Coupe, 1997). Conversely, Weatherhead and Anderka (1984) reported that radiotelemetered black rat snakes (*Elaphe obsoleta*) moved to sheltered areas for 1–18 d immediately following surgery and release. During the May–August session of our study, movements were significantly greater 6–14 d after snakes were released than 15–21 or 22–30 d after release. During the January–March session, we did not begin tracking the snakes until 2 weeks after we released them.

BTS moved extensively during any given night but over the course of each seasonal period tended to concentrate their movements within core areas. Snakes moved an average total cumulative distance of almost 240 m between successive locations from one afternoon to the next during January–March and 180 m during May–August. However, over the course of the 4–5 wk that we monitored movements during each seasonal period, the median distance of all locations from each snake's central point was <60 m. The spatial analyses confirmed that individual snakes consistently inhabited the same core areas throughout the 4–5 wk of each seasonal period. The mean distance of snakes from their original release points 30–50 d and 60–70 d after release was <95 m during each of two seasonal periods. Several other species of snake that also inhabited restricted home ranges for several weeks or longer subsequently made major movements away from their starting points (Fitch and Shirer, 1971; Michot, 1981). More study would be required to determine whether movements by BTS in our study increased after the 9–10 wk that we monitored their movements.

Snake movements often vary by sex, reproductive condition, and season. For instance, females of many species of viviparous snakes are sedentary during gestation (Gregory et al., 1987; Charland and Gregory, 1995), probably to reduce predation or regulate body temperature. Movements in our study varied little between sexes or between adults and subadults, but were slightly more extensive during January–March than during May–August.

Snake movements often are related to variation in the abundance and dispersion of critical resources (Gregory et al., 1987). Several studies have documented the effect of prey density on snake movements (Duvall et al., 1985; Gibbons and Semlitsch, 1987; Gregory et al., 1987). Santana-Bendix et al. (unpubl. data) observed relatively large home ranges of BTS in Guam and speculated that snakes traveled extensively to find food because the prey base was collapsing. The snakes in our study moved considerably less, perhaps because (1) prey were more abundant, (2) BTS in our study were smaller and required fewer or smaller prey, or (3) other ecological shifts occurred during the intervening period. Also, we tracked snakes intensively for only 30–40 d, compared to an average of 48 d for Santana-Bendix et al. (unpubl. data). BTS (Santana-Bendix et al., unpubl. data) and other species of snakes (Barbour et al., 1969; Fitch and Shirer, 1971; Michot, 1981) often remain in a home area from several days to weeks before making a major movement to a new area, perhaps in response to food depletion and the need to find more abundant prey.

Activity.—BTS on Guam apparently have shifted their diel activity cycle from being almost totally nocturnal to being more crepuscular. Between 1978 and 1984, >90% of electrical outages caused by BTS occurred between 1800 h and 0559 h; morning outages were relatively rare during this period (Fritts et al., 1987). By 1989–91, nocturnal electrical outages had declined to <50% of the total, and early morning outages had increased substantially (Fritts and Chiszar, 1998). The investigators attributed this extension of nocturnal foraging into the morning hours to a collapse of forest bird and introduced mammal populations and a need for snakes to forage over larger areas for longer periods. Our study confirms that BTS are primarily nocturnal, although we cannot determine from our data the extent of early morning foraging.

Fritts et al. (1987) analyzed snake-caused power outages over an 8 yr period as an index of snake activity and abundance and found that the incidence of power outages caused by snakes was maximal during May, June, and July, which usually corresponds with the beginning of the rainy season. Our intensive nightly observations extended only into the first week of July. That the rainy season during this study did not commence until mid-July may have accounted for the lack of increased nightly, weekly, or seasonal movements during the May-August seasonal period.

Management Implications.—The proper density and placement of control devices such as traps, lures, or poison baits needed to reduce populations of BTS are contingent on the mobility and behavior of the animals. The more extensive the movements, the more traps or baits a snake is likely to encounter. The heights of refugia and nightly movements observed in this study indicate that traps, baits, or other devices probably should be placed within 3.5 m of the ground at <60-m intervals to ensure that every BTS has an opportunity to encounter one. This requirement did not vary between the two seasonal periods when this study was conducted. Traps should be placed in forests because snakes tend to avoid grassy open areas. Snake movements likely would vary in other habitats with different species and densities of prey.

Engeman et al. (1998c) suggested that operational trapping can remove virtually all snakes from fragmented forested habitats, and Engeman and Linnell (*in press*) observed slow recovery of BTS populations in such areas. The restricted movements observed in this study also indicate that BTS would be slow to reinvade such areas. Nonetheless, snake activity should be monitored closely because populations and movements can vary widely in response to changing social and environmental factors (Rodda et al., 1992). BTS in our study moved as far as 259 m between refugia used on successive days. The dirt and limestone roads in our study area did not constrain BTS movement; both adults and juveniles of both sexes crossed roads frequently. That we located snakes in grassy clearings less frequently than one would expect from the percentage of the study area that comprised such areas suggests that such areas may be partial impediments to dispersal. Arboreal snakes such as BTS probably are more vulnerable to predation when they move across large open areas (Shine and Fitzgerald, 1996). More study is needed to determine the optimum buffer width that would deter BTS from dispersing into shipping ports, warehouses, or other high risk areas that serve as sources of stowaways for the accidental transport of BTS from Guam.

Acknowledgments.—The U.S. Department of Defense Legacy Project Number 1281 provided the funding for this study. M. Pitzler allowed use of USDA/WS facilities on Guam and provided other logistic support. D. Rodriguez and his USDA/WS crew captured the BTS used in this study. A. E. Haun and L. W. Workman of PHRI kindly permitted use of data from their GPS base station to differentially correct our GPS data. J. Brooks, R. Bruggers, A. Dale, S. Fancy, and G. Rodda reviewed the study protocol and advised on study methods. H. Hirsh facilitated approval for conducting the study on AAFB and access to the Munitions Storage Area. E. Campbell, B. Coup, R. Engeman, M. Fall, T. Fritts, R. Henderson, G. Rodda, J. Shivik, and an anonymous reviewer commented on earlier drafts of this manuscript.

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Accepted: 31 January 1999.